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THE EFFECT OF SEASONALITY OF BURN ON SEED GERMINATION IN CHAPARRAL: THE ROLE OF SOIL MOISTURE

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Abstract

Fire represents an important recruitment phase for many chaparral species. Prescribed burns are often scheduled during winter or spring when soil moisture is high in order to minimize risks of uncontrolled fire. However, chaparral wildfires typically occur in the summer or fall when soil moisture is low. Changing the seasonality of burn affects pre-burn soil moisture, burn temperature and timing of germination. High soil moisture during winter or spring burns is hypothesized to lower germination rates of chaparral plants compared to fall burns. The purpose of this study was to evaluate the effects of prescribed spring burns on the germination of chaparral species in the Mendocino National Forest, California. We conducted two experiments to test for effects of moisture on seed germination. In the soil heating experiment, soil collected under chaparral was heated at several temperatures and soil moistures, and germinating seeds were counted. In the seed heat treatment experiment, seeds of 13 species were heated moist and dry to determine the moisture effect on heated seeds. Results indicate a differential response of seeds to heat and soil moisture. *Lotus humistratus, Daucus pusillus* and *Penstemon heterophyllus* were negatively affected by temperature in both moist and dry treatments. *Ceanothus cuneatus* and *Genista monspessulana* germination increased with temperature in both dry and moist treatments. Germination of six species (*Adenostoma fasciculatum, Camissonia contorta, Emmenanthe pendiflora, Epilobium ciliatum, Galium aparine* and *Malacothrix clevelandii*) decreased under moist heat treatments. These results suggest that spring burns may lead to decreased diversity of chaparral due to reduced seed survival and germination of certain species.

Key Words: seasonal burns, chaparral, soil moisture, temperature, seed germination, prescribed burns, seed bank.

Fire has become an important management tool, to recreate or maintain specific vegetation communities (oak savanna, grassland, southeastern pine forest, tall grass prairie, chaparral), to maintain species diversity and endangered or rare species, and to control invasive species (Zedler and Scheid 1988; Minnich 1989; Keeley 1991). Fire as a biological process consists of a complex set of components (timing, intensity, duration, interval between burns), and "fire adapted" vegetation is typically adapted to a specific set of ranges of these components. Shifting the timing of fire can substantially affect vegetation structure, vegetation composition and the soil seed bank of a site (Kauffman and Martin 1991). In chaparral, the previously dormant soil seed bank is an important post-fire recruitment source (Keeley 1987). A better understanding of the effect of seasonality of burn on species diversity and seed bank composition would improve the ability of land managers to incorporate fire into management plans.

Chaparral structure and composition is greatly influenced by fire (Moreno and Oechel 1991). Chaparral is an evergreen sclerophyllous shrub vegetation that dominates in moderately xeric sites of California that are characterized by seasonal drought (Christensen and Muller 1975a). The combination of dense shrub cover, severe summer drought and the accumulation of "fuel" in chaparral lead to frequent fires, with frequencies of once every 40 to 60 years in southern California (Christensen and Muller 1975b). Fires represent an important recruitment phase for many chaparral species: Diversity and seedling numbers are highest in the first and second growing seasons after fire (Christensen and Muller 1975b). Recruitment may be affected by changes in the fire regime, such as fire exclusion or very frequent fires (Keeley 1995; Zedler 1995; Keeley 2002).

In chaparral, winter and spring prescribed burns change some components of the fire regime. In particular, changing the seasonality of the burn from the fall to the spring affects soil moisture, timing of regrowth, and fire intensity (Parker 1990). Since seed response to heat and soil moisture varies according to seed water absorption, the seasonality of burn and soil moisture content can greatly influence germination patterns.

Timing of burns also has the potential to change the invasion regime of post-fire alien species (Kauffman and Martin 1991). For example, burning in early summer, just as plants begin to flower, prevents seed production of yellow star-thistle (*Centaurea solstitialis* L. [Asteraceae]) in grasslands in

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California. However, late spring and fall burns increase diversity of native species and decrease abundance of alien species (Hastings and DiTomaso 1996). In some cases, fire may allow invasive species like *Cytisus scoparius* L. (Fabaceae) and *Carpobrotus edulis* (Aizoaceae) to increase in numbers (Zedler and Scheid 1988; D'Antonio et al. 1993; Agee 1996). Thus, management strategies involving fire must take into account the mix of individual species with different life histories and responses to fire and the phenological timing of burns (Parker 1990; Glitzenstein et al. 1995; Spier and Snyder 1998).

Previous studies have examined the effect of heat on the seed response of chaparral species (Keeley and Nitzberg 1984; Keeley et al. 1985), but few studies have examined the effect of changing the seasonality of burn and soil moisture on seed germination at the time of fire. Understanding the effect of soil moisture at the time of fire can help predict the effect of burns on responses of individual species and the resulting species composition of the chaparral.

An important step in managing vegetation with fire is to classify taxa into ecological response groups, keeping in mind that each species has unique life history characteristics (Parker 1990). Two functional groups can be distinguished within a seed bank: Species that do not require fire for germination (fire-independent), and species which are fire-stimulated either via heat, smoke chemistry or some other mechanism (Parker and Kelly 1989; Zammit and Zedler 1994). Fire-stimulated seeds are adapted to surviving the heat produced in a fire, and represent about 21% of the total seed bank in chaparral (Zammit and Zedler 1994). Fire-independent seeds comprise almost 2/3 of the total seed bank in mixed chaparral; these species can potentially recruit at any point in the fire cycle, including immediately after fire (Zammit and Zedler 1994). Seeds of obligate resprouters, geophytes, perennial grasses and many introduced annuals are non-dormant and fire-independent (Zammit and Zedler 1994).

In California chaparral, higher rates of seed germination occur following autumn fires than spring fires (Parker and Kelly 1989). In laboratory experiments, germination is negatively affected for many species heated under moist conditions typical of spring burns (Rogers et al. 1989). Seeds lacking hard seed coats have lower heat tolerance after they have absorbed moisture (Parker 1990). Spring and winter burns, typically of lower heat intensity, may have a negative impact on species with hard seed coats that require high temperatures to germinate (e.g., *Ceanothus*) (Parker 1990).

The goal of this study was to examine the impact on the seed bank of spring prescribed burns in California chaparral. Our objectives were to determine the effect of changes in soil moisture and temperature during spring burns on seed germination in the chaparral vegetation of the Mendocino National Forest, California. In order to examine seed bank response to soil moisture and heat treatments, we conducted two experiments. In the first experiment, germination was measured in soil heated in the laboratory under several moisture conditions. In the second experiment, seeds of selected species were heated dry and after imbibing water to determine moisture effects on specific species. Heat treatments were selected to duplicate soil temperatures during a burn (70°C to 110°C). Soil moisture treatments included expected summer soil moistures (3% to 7%) and possible spring soil moistures (17–30%).

Methods

We obtained soil and seeds from the east slope of the Coast Range Mountains, in previously burned chaparral, in the Mendocino National Forest, in northern Glenn County, near Highway 162, north-west of Elk Creek, California USA (122°7′W, 39°72′N). The vegetation consisted primarily of *Adenostoma fasciculatum* Hook. & Arn. (Rosaceae) and *Ceanothus cuneatus* var. *cuneatus* (Hook.) Nutt. (Rhamnaceae). Soil samples were collected from the upper 5 cm of soil under mixed *Ceanothus* and *Adenostoma* chaparral in August 1994. All seeds except *Genista monspessulana* (L.) L. Johnson (Fabaceae) were collected in the Mendocino National Forest in 1994 and 1995. *Genista* seeds were collected from Old Railroad Grade on Mount Tamalpais in Marin and were selected for this experiment because its seeds are known to imbibe less than 5% of their dry weight, and the species is an invasive in chaparral.

Soil Experiment

We moistened the soil, and placed it in ziplock bags for one week to ensure even moistening. We conducted four heat treatments (control [unheated], 90°C, 100°C, and 110°C) and five moisture treatments (3%, 15%, 22% and 30% of soil dry weight), with four replicates per treatment. The soil was heated for 10 minutes in an oven, using soil probe thermometers to measure soil temperature. Samples were stratified at 5°C to 8°C for two weeks then placed in the greenhouse and 50 ml of charate (as per Keeley 1987) was added to each flat (20 cm × 20 cm). We monitored germination every two weeks over the course of 120 days.

Seed Experiment

We examined the effect of temperature on dry and moistened seeds of thirteen species: *Adenostoma fasciculatum*, *Ceanothus cuneatus* var. *cuneatus*, *Penstemon heterophyllus* Lindley (Scrophulariaceae), *Camissonia contorta* (Douglas) Raven (Onagraceae), *Mentzelia dispersa* S. Watson (Loasaceae), *Galium aparine* L. (Rubiaceae), *Daucus pusillus* Michaux (Apiaceae), *Malacothrix cleve-*

TABLE 1. MEAN NUMBER OF SEEDLINGS PER FLAT IN RESPONSE TO HEAT AND MOISTURE TREATMENTS IN SOIL COLLECTED IN CHAPARRAL IN THE MENDOCINO NATIONAL FOREST, CALIFORNIA. Values are mean numbers of seedlings per flat (SD) for each species (n = 4). Results of Kruskal-Wallis test followed by multiple range analysis on ranks. AB (within a row) represents moisture effect (result of comparison among moisture treatments within a temperature treatment); ab (within a column) represents heat effect within a soil moisture treatment (results of comparison among heat treatments). Treatments with the same letter are not significantly different. * $P < 0.05$; ** $P < 0.01$.

	# Seedlings per flat (SD) Soil moisture				Moisture effect	
	3%	15%	22%	30%	P	χ^2
Control: no heat						
Adenostoma fasciculatum	4.75 (1.89)	3.25 (1.70)^{a**}	4.66 (0.58)^{a**}	4.75 (2.5)^{a**}	0.32	3.47
Ceanothus cuneatus	0	0.75 (0.5)^{c*}	1.33 (2.33)^{c}	0.75 (0.96)^{b*}	0.32	3.48
Eriodictyon californicum	0.5 (1.00)^{b**}	0.25 (0.5)	0^{a**}	2.5 (1)^{a**}	0.12	5.8
Gnaphalium californicum	0.25 (0.5)	0	0	0	0.43	2.8
Isopyrum stipitatum	0.25 (0.5)	0.25 (0.5)	0	0	0.6	1.9
Navarretia pubescens	0	0.25 (0.5)	0	0	0.43	2.8
Unknown	0.25 (0.5)	0.5 (0.58)	0	0.25 (0.5)	—	—
Verbascum thapsus	0	0	0	0.25 (0.5)	—	—
Total Density	5.75 (3.30)^{b**}	6.25 (4.03)	7.33 (2.31)	8.5 (3.32)	0.68	1.5
90°C						
Adenostoma fasciculatum	1.75 (0.96)^{A}	0^{B}	0^{b}	0$^{B\ b}$	0.002	14.7
Ceanothus cuneatus	0.75 (0.96)^{B}	5.75 (1.70)$^{A\ a}$	6.5 (2.6)$^{A\ a}$	5.5 (2.38)$^{A\ a}$	0.04	8.3
Eriodictyon californicum	0.5 (1.0)^{b}	0.25 (0.5)	0	0^{b}	0.54	2.2
Total Density	2.75 (1.71)^{b}	6 (2.16)	6.5 (2.64)	5.5 (2.38)	0.16	5.2
100°C						
Adenostoma fasciculatum	4 (2.16)^{A}	0$^{B\ b}$	0$^{B\ b}$	0$^{B\ b}$	0.003	13.6
Ceanothus cuneatus	1 (1.41)	2.5 (2.64)$^{a\ b}$	2.5 (1.29)$^{b\ c}$	4.5 (2.38)^{a}	0.12	5.9
Eriodictyon californicum	29 (18.16)$^{A\ a}$	0^{B}	0$^{B\ b}$	0$^{B\ b}$	0.004	13.6
Gnaphalium californicum	0.25 (0.5)	0	0	0	—	—
Total Density	34.25 (19.96)$^{A\ a}$	2.5 (2.65)^{B}	2.5 (1.29)^{B}	4.5 (2.38)^{B}	0.02	9.4
110°C						
Adenostoma fasciculatum	5 (3.46)^{A}	0$^{B\ b}$	0$^{B\ b}$	0$^{B\ b}$	0.007	12.1
Camissonia contorta	0.25 (0.75)	0	0	0	—	—
Ceanothus cuneatus	1.75 (1.70)	2.5 (1.91)	5.25 (2.06)$^{a\ b}$	1.75 (1.71)$^{a\ b}$	0.16	5.1
Eriodictyon californicum	26.75 (20.15)$^{A\ a}$	0^{B}	0$^{B\ b}$	0$^{B\ b}$	0.004	13.6
Total Density	33.75 (18.41)$^{A\ a}$	2.5 (1.91)^{B}	5.25 (2.06)^{B}	1.75 (1.71)^{B}	0.02	10.3

TABLE 2. PERCENT WATER ABSORPTION ([MOIST WEIGHT − DRY WEIGHT]/DRY WEIGHT) FOR SEEDS SOAKED 8 HOURS IN DISTILLED WATER.

Species	Percent water absorption
Adenostoma fasciculatum	49.7
Camissonia contorta	70.0
Ceanothus cuneatus	4.2
Daucus pusillus	43.0
Dicentra chysantha	25.1
Emmenanthe pendiflora	46.7
Epilobium ciliatum	187.0
Gallium aparine	65.5
Genista monspesullana	0.0
Lotus humistratus	81.0
Malacothrix clevelandii	86.1
Mentzelia dispersa	5.5
Penstemon heterophyllus	71.3

landii A. Gray (Asteraceae), *Dicentra chrysantha* (Hook. and Arn.) Walp. (Papaveraceae), *Epilobium ciliatum* ssp. *ciliatum* Raf. (Onagraceae), *Emmenanthe penduliflora* var. *penduliflora* Benth. (Hydrophyllaceae), *Lotus humistratus* E. Greene (Fabaceae) and *Genista monspessulana* (L.) L. Johnson (Fabaceae).

We completed two sets of seed heat treatments: a set with pre-soaked seeds (soaked in distilled water for eight hours prior to heating) and a set with dry seeds. Seeds were heated in glass tubes in an oil bath heater containing sand for 10 minutes at 70°C, 90°C and 110°C. Temperature probes measured the heat in the tubes. One control set was not heated. After heat treatment, we placed seeds in Petri plates (25 seeds per plate) between two layers of Whatman no. 1 filter paper, and applied a 5 ml aqueous solution of charate, prepared as per Keeley (1987), then stratified seeds in an incubator. Petri plates were examined weekly for germination for up to 14 weeks, and germinated seeds were counted and removed.

Seeds of different species were stratified at specific combinations of light and temperature to maximize germination (Keeley and Keeley 1987; V.T. Parker, unpublished data). The seeds of *Adenostoma, Ceanothus, Malacothrix, Dicentra, Emmenanthe, Daucus, Galium* and *Epilobium* were stratified in the dark at 5°C for 3 weeks, then for 4 weeks with 12 hours of light (20°C) and 12 hours of darkness (5°C). This cycle was repeated once in order to maximize germination rates. *Camissonia, Penstemon* and *Mentzelia* seeds were first stratified in the dark (5°C) for 3 weeks, then with 12 hours of light (20°C) and 12 hours of darkness (5°C) for 4 weeks. For the second cycle they were placed at 30°C (dark) for 1 week, then at a regime of 12 hours of light and 12 hours of dark for 2 weeks. *Genista* and *Lotus* were stratified for 4 weeks in the dark at 5°C, then at 10 hours light (20°C) and 14 hours dark (5°C) for 3 weeks.

Data Analysis

We used a Kruskal-Wallis analysis followed by a multiple range analysis on ranks to compare germination of soil burn treatments (SAS 2004). For each species, we compared percentage germination for heat and moisture treatments with a two-way Analysis of Variance after arc-sine transforming the data, followed by multiple pair-wise comparisons (Tukey) to determine differences between moisture treatments and between control and heat treatments (SAS 2004).

RESULTS

Soil Experiment

Germination in soil heated under dry conditions (i.e., 3% soil moisture) varied among species. At 3% soil moisture, *Eriodictyon* germination increased significantly with heat ($P < 0.01$) (Table 1). Total density reflected the high germination of *Eriodictyon* (Table 1). *Eriodictyon* germinated in small quantities in the control and 90°C treatments (0.5 per flat); its densities increased significantly and were very high at 100°C and 110°C, reaching a high of 29 seedlings/flat at 100°C ($P < 0.01$) (Table 1). In contrast, *Ceanothus* and *Adenostoma* germination did not increase with heat (Table 1). For *Gnaphalium californicum* DC. (Asteraceae), *Isopyrum stipitatum* A. Gray (Ranunculaceae), *Navarretia pubescens* (Benth.) Hook. and Arn. (Polemoniaceae), and *Verbascum thapsus* L. (Scrophulariaceae), germination was too low to examine statistically (Table 1).

Eriodictyon, Adenostoma and total germination were negatively affected by heat under moist conditions (i.e., 15%, 22% and 30% soil moisture) (Table 1). *Eriodictyon* germination was significantly lower under moist conditions at soil temperatures of 100°C and 110°C ($P \leq 0.01$) (Table 1). *Adenostoma* germination decreased under moist conditions when the soil was heated ($P \leq 0.01$) (Table 1).

Total density decreased as temperature and soil moisture increased (Table 1). At low temperatures (no heat and 90°C), total density was not affected by soil moisture ($P > 0.05$) (Table 1). However, total density decreased significantly in moist soil at temperatures of 100°C and above ($P < 0.05$) (Table 1).

At 90°C, *Ceanothus* germination was higher under moist conditions (Table 1). At other temperatures, soil moisture did not affect *Ceanothus* germination. *Ceanothus* was the only species germinating in moist soil at temperatures above 90°C (Table 1).

Seed Experiment

Seed water absorption, as percent of dry weight ([moist weight − dry weight]/dry weight) ranged from 4% to more than 100% of their dry weight

TABLE 3. RESULTS OF TWO-WAY ANOVA FOLLOWED BY MULTIPLE PAIR-WISE COMPARISONS (TUKEY) TO DETERMINE THE EFFECT OF HEAT AND MOISTURE TREATMENTS ON PERCENTAGE GERMINATION OF SEEDS COLLECTED IN CHAPARRAL IN THE MENDOCINO NATIONAL FOREST, CALIFORNIA. Values are mean and standard deviation (SD) of percent germination. * indicates significant difference ($P < 0.05$) between heat treatment and control.

	Heat treatment									
	Control		70°C		90°C		110°C		Heat effect	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	*P*	*F*
Adenostoma fasciculatum (n = 8)										
Dry Treatment	20	4	22	11	30	12	1	1	<0.001	22.8
Moist Treatment	19	9	2*	4	0*	0	0*	0		
P (dry vs moist)			<0.001		<0.001					
Camissonia contorta (n = 4)										
Dry Treatment	6	5	63*	11	47*	14	35*	24	0.001	7.1
Moist Treatment	9	3	2	4	0	0	0	0		
P (dry vs moist)			<0.001		<0.001		0.004			
Ceanothus cuneatus (n = 8)										
Dry Treatment	0	0	3	4	9	5	25*	17	<0.001	16.0
Moist Treatment	1	1	8	11	20*	10	20*	15		
P (dry vs moist)										
Daucus pusillus (n = 8)										
Dry Treatment	35	15	6*	7	1*	2	0*	0	<0.001	85.1
Moist Treatment	32	10	0.5*	1	0*	0	0*	0		
P (dry vs moist)										
Dicentra chrysantha (n = 4)										
Dry Treatment	0	0	0	0	0	0	3	7	0.13	2.1
Moist Treatment	0	0	3	3	0	0	1	1		
P (dry vs moist)										
Emmenanthe penduliflora (n = 8)										
Dry Treatment	58	17	55	7	3*	4	40	17	<0.001	84.2
Moist Treatment	65	17	1*	1	1*	1	0*	0		
P (dry vs moist)			<0.001				<0.001			
Epilobium ciliatum (n = 8)										
Dry Treatment	57	8	55	10	45	15	15*	3	<0.001	112.5
Moist Treatment	53	17	5*	1	1*	2	0*	0		
P (dry vs moist)			<0.001		<0.001					
Galium aparine (n = 8)										
Dry Treatment	58	11	52	13	25*	11	3*	4	<0.001	131.5
Moist Treatment	61	13	0*	0	0*	0	0*	0		
P (dry vs moist)			<0.001		<0.001					

TABLE 3. CONTINUED.

Species	Heat treatment									
	Control		70°C		90°C		110°C		Heat effect	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	*P*	*F*
Genista monspesullana (n = 8)										
Dry Treatment	15	3	23*	1	23*	1	<0.001	81.9		
Moist Treatment	14	2	23*	2	26*	2				
P (dry vs moist)										
Lotus humistratus (n = 4)										
Dry Treatment	13	2	24	15	3	4	3	4	<0.001	11.2
Moist Treatment	31	7	18	14	7*	7	4*	6		
P (dry vs moist)	0.02									
Malacothrix clevelandii (n = 4)										
Dry Treatment	81	5	64*	12	5*	5	1*	2	<0.001	390.5
Moist Treatment	78	5	0*	0	0*	0	0*	0		
P (dry vs moist)			<0.001							
Mentzelia dispersa (n = 4)										
Dry Treatment	1	3	2	3	3	4	2	2	0.66	0.5
Moist Treatment	1	2	0	0	1	2	2	4		
P (dry vs moist)										
Penstemon heterophyllus (n = 4)										
Dry Treatment	10	4	0*	0	0*	0	0*	0	<0.001	26.2
Moist Treatment	11	6	0*	2	0*	0	0*	2		
P (dry vs moist)										

(Table 2). *Ceanothus, Genista,* and *Mentzelia* seeds imbibed 4% or less of their dry weight in water. All other seeds absorbed 23% or more of their dry weight.

Three species (*Ceanothus, Genista* and *Camissonia*) showed a positive temperature effect on germination when heated dry (Table 3). *Ceanothus* germination increased from 0 at the control temperature to 25% at 110°C. *Genista* germination increased from 15% at no heat to 23% when heated. Germination of *Camissonia* seeds increased from 6% when unheated to as much as 63%.

In eight species, *Adenostoma, Emmenanthe, Epilobium, Galium, Daucus, Lotus, Malacothrix* and *Penstemon,* at least one heat treatment under dry conditions negatively affected germination (Table 3). Heat tolerance of species varied, but germination of all of the former species except *Emmenanthe* dropped at 110°C. *Daucus* and *Penstemon* were most sensitive to heat: germination dropped at 70°C. *Emmenanthe, Galium* and *Lotus* germination dropped at temperatures of 90°C. *Epilobium* was most tolerant of heat: germination dropped significantly at 110°C.

Germination of five species (*Ceanothus, Genista, Lotus, Daucus* and *Penstemon*) was not affected by moisture (Table 3). *Lotus, Daucus* and *Penstemon* seeds were negatively affected by temperature in both moist and dry treatments (Table 3). *Ceanothus* and *Genista* germination was higher when seeds were heated in both moist and dry treatments (Table 3).

Germination of six species (*Adenostoma, Camissonia, Emmenanthe, Epilobium, Galium, Malacothrix*) decreased under moist heat treatments at temperatures as low as 70°C (Table 3).

Discussion

Levels of heat tolerance vary among species (Keeley et al. 1985; Keeley 1987; Keeley and Keeley 1987; Odion and Davis 2000), and high temperatures (150°C) can be lethal for seeds (Keeley et al. 1985; Cruz et al. 2003). For several fire-stimulated species in this study, germination decreased at 120°C.

The heat-stimulated seed germination (heat or chemical cues) observed in many species in this study (*Ceanothus, Camissonia, Lotus, Genista, Emmenanthe*) supports findings in other field and laboratory studies (Keeley and Nitzberg 1984; Keeley et al. 1985; Keeley and Keeley 1987; Moreno and Oechel 1991; Ferrandis et al. 1999). Also, *Adenostoma* has previously been observed to be sensitive to heat during winter burns (Moreno and Oechel 1991).

Soil moistures of 15%, equivalent to those occurring during spring burns in the Mendocino National Forest, had a negative impact on seeds with no seed coat dormancy (Le Fer 1998). Seeds that were negatively impacted by heat under moist conditions (*Adenostoma, Camissonia, Galium, Epilobium, Malacothrix, Emmenanthe*) had no seed coat dormancy and absorbed water above 23% of their weight. These included seeds of opportunistic "fire survivors" that do not require fire to germinate and may survive low intensity heat (e.g., *Adenostoma, Epilobium, Galium*). A group of fire-sensitive postfire colonizers was sensitive to any amount of heat, moist or dry (*Emmenanthe, Daucus*).

Conditions during spring prescribed burns may be conducive to germination of fire-stimulated seeds with seed coat dormancy (e.g., *Ceanothus, Genista*). Hard-coated seeds absorbed 4% or less of their weight in water and did not exhibit a negative temperature effect under moist conditions. *Ceanothus,* an obligate seeding shrub, may increase in numbers after spring burns. However, some spring burns may not reach temperatures high enough to stimulate *Ceanothus* seed germination (Parker 1989). Assuming seed longevity of about 50 years, any ungerminated seeds might die before the next fire (Parker 1989; O'Neil 2002), leading to decreased seed bank diversity. *Ceanothus* reaches sexual maturity at 20 years of age, at which time seed banks reach their highest levels (Zamitt and Zedler 1994). Ungerminated seeds are also susceptible to predation (Mills and Kummerow 1989; O'Neil 2002).

Seeds of shrub species that would germinate under the low moisture conditions typical of fall burns (e.g., *Eriodictyon* and *Adenostoma*), are negatively affected under conditions found during spring burns. *Adenostoma* may continue to dominate postfire vegetation by resprouting. However, without the establishment of younger plants by germination, shrub density will eventually decline.

Diversity in the chaparral community is retained primarily within the seed bank (Sampson 1944; Sweeney 1956; Keeley and Keeley 1987; Parker and Kelly 1989). Spring prescribed burns may change the composition of the seed bank over time by differentially promoting germination of species with hard-coated seeds over those with soft-coated seeds. High soil moistures during burns negatively affect germination for many species that would survive fall burns, and this would likely lead to shifts in community composition. The impact of winter or spring burns may be particularly severe for fire-dependent herbaceous annuals with soft seed coats (e.g., *Emmenanthe, Epilobium*), since their seeds wouldn't survive fires under wet conditions, and may be depleted from the seed bank.

Fire can promote invasion of nonnative species (Zedler and Scheid 1988; D'Antonio et al. 1993). A late spring fire leads to germination the following spring, leaving an opportunity for nonnative species to disperse to and establish at the site (Parker 1989). The reduction in density and species richness of plants germinating from dormant seed banks also can give nonnative species an opportunity to become established (Parker 1989). Seeds of some nonnative species (e.g., *Genista*) may germinate at high rates after spring fires, leading to increased eradication difficulties. The European invasive *Genista* can resprout after fire, and produces a large and persistent seed bank (Parker and Kersnar 1989), stimulated by moderate heat either from fire or summer heat (Parker 1993; Ferrandis et al. 1999).

Burns are an important component of chaparral management and many species require fire to germinate. However, shifting the fire regime to the winter or spring affects soil moisture, fire intensity and timing of germination. Burning during the dry season maintains historical fire regimes and thus decreases these alterations to the ecosystem's dynamics. If this is not feasible, selecting prescribed burn windows that minimize soil moisture may decrease negative impacts. In addition, post-fire monitoring of regeneration and community composition can provide information that increases our understanding of the effects of environmental variables (e.g., moisture, heat, time of year) on specific species.

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